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Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems

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The effects of biodiversity on ecosystem functioning generally increase over time, but the underlying processes remain unclear. Using 26 long-term grassland and forest experimental ecosystems, we demonstrate that biodiversity–ecosystem functioning relationships strengthen mainly by greater increases in functioning in high-diversity communities in grasslands and forests. In grasslands, biodiversity effects also strengthen due to decreases in functioning in low-diversity communities. Contrasting trends across grasslands are associated with differences in soil characteristics.

More than two decades of research have revealed that biodiversity is a significant driver of ecosystem functioning[1,2]. Positive biodiversity effects on ecosystem functioning have been found in grassland and forest biodiversity experiments[3,4], with growing evidence showing that biodiversity–ecosystem functioning relationships may become stronger over time[5–7]. Moreover, several recent studies have suggested that long-term biodiversity effects in experiments better mirror natural conditions than short-term studies and likely help explain biodiversity–ecosystem functioning relationships in real-world ecosystems[8–11].

Temporal increases in plant diversity effects on ecosystem functioning may result from an increase in functioning in high-diversity communities[7], a decrease in functioning in low-diversity communities[12] or both. However, it remains unknown which of these trends drives temporal increases in diversity effects on ecosystem functioning, whether these trends are consistent across experiments and ecosystems, and if not, whether context dependency in temporal trends may be attributed to site conditions. For instance, soil characteristics likely influence the biodiversity–ecosystem functioning relationship[10,13,14] and may influence temporal trajectories as well, but whether or not they do so is unclear.

Understanding the temporal trends of biodiversity effects on ecosystem functioning is critical for providing insights into biodiversity–ecosystem functioning relationships[9,15] and predicting the potential consequences that progressive biodiversity change[16,17] and management[18,19] might have on ecosystem functioning and service provisioning over time. Furthermore, examining these temporal trends is fundamental for guiding research on understanding the underlying mechanisms (for example, a variety of niche-differentiation processes, such as complementary resource use and facilitation, which can have positive effects on the functioning of high-diversity communities[6,20], and the impact of pests and diseases, which can have negative effects on the functioning of low-diversity communities[9]).

In this study, we examined temporal shifts in biodiversity effects on ecosystem functioning in terrestrial ecosystems—specifically, plant diversity effects on plant above-ground biomass in grassland and on the basal area in forest experimental ecosystems. We used data from 26 long-term biodiversity experiments that manipulated plant species richness in grasslands (14 experiments) and forests (12 experiments) (Supplementary Table 1). We investigated whether the strength of the biodiversity–ecosystem functioning relationship increases with time and whether temporal divergence across plant richness levels is driven by an increase in function in high-diversity communities, a decrease in function in low-diversity communities or a combination of both. Finally, when temporal trends differed across experiments, we assessed the potential role of soil characteristics in shaping these temporal trends.

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In grasslands, the relationship between plant species richness and plant above-ground biomass was positive and became significantly stronger over time (Supplementary Table 2 and Fig. 1a). Temporal divergence across plant richness levels was observed in 10 out of 14 grassland experiments (Supplementary Fig. 1). Although temporal divergence was frequently associated with more diverse communities showing stronger increases in plant above-ground biomass over time (Fig. 1a), the temporal increase of diversity effects was not determined by a consistent trend across studies (see variance components in Supplementary Table 2): temporal divergence was driven by a decrease in function in low-diversity communities in one experiment, by an increase in function in high-diversity communities in six experiments and by a combination of both in three experiments (Supplementary Fig. 1).

The context dependency underlying biodiversity–ecosystem functioning relationships in grasslands were strongly associated with variation in soil characteristics across the experiments (Supplementary Table 3). Soils influenced biodiversity–ecosystem functioning relationships in two ways. First, the interaction between soil characteristics related to soil texture and pH (soil PC2) and plant species richness shaped the overall richness effect (significant richness × soil PC2 interaction; Supplementary Table 3 and Supplementary Figs. 2 and 3). Second, soil characteristics, such as the cation-exchange capacity, soil organic carbon, water content at the wilting point and bulk density (soil PC1) contributed to driving temporal divergence (significant richness × time × soil PC1 interaction; Supplementary Table 3, Fig. 2 and Supplementary Fig. 2). Temporal divergence driven by an increase in function in high-diversity communities was associated with studies located in areas with higher cation-exchange capacity, soil organic carbon and water content and lower bulk density, while a decrease in function in low-diversity communities was associated with the the inverse pattern (that is, lower cation-exchange capacity, soil organic carbon and water content and higher bulk density; Fig. 2).

The general increase in the biodiversity–ecosystem functioning relationship through time was due to contrasting trajectories across grassland studies, showing the importance of context-dependency of the biodiversity–ecosystem functioning relationship in this ecosystem. Our analyses reveal that soil characteristics contribute to strengthening plant species richness effects on ecosystem functioning in general and through time in multiple ways. First, variability in ecosystem functioning across plant species richness levels was generally lower in experiments with sandy soils. Second, temporal divergence was explained by stronger increases in ecosystem function in high-diversity compared with low-diversity communities in experimental sites with higher soil organic carbon, whereas temporal divergence in experimental sites with low soil organic carbon was explained by a decrease in ecosystem function in low-diversity communities. Therefore, the influence of resource availability on plant–plant interactions as well as multi-trophic interactions[21] may underlie temporal changes in biodiversity effects[10,13] and related mechanisms[14,22]. It is also likely that other abiotic and biotic factors play a role in shaping the biodiversity–ecosystem functioning relationship through time. For instance, most of the grassland biodiversity experiments were perennial dominated (more than 75% of the species were perennial), except for the BIODEPTH Greece and Portugal sites (less than 30% of the species were perennial), where there was no evidence of temporal divergence. Grassland experiments dominated by annual plants may be strongly affected by processes related to recruitment, such as seed availability (either from their own plot or surrounding plots) and microsites[23]. Recruitment may influence diversity effects in grasslands, mainly due to changes in plant density rather than changes in plant size[24].

In forests, plant richness effects on the periodic annual increment of the basal area were consistently positive across the studies (see variance components in Supplementary Table 2, Fig. 1b and Supplementary Fig. 4) and, in contrast with grasslands, we did not find evidence that they changed over time (neither time nor richness × time was significant; Supplementary Table 2 and Fig. 1b). Consequently, the temporal divergence of the total basal area among tree species richness levels depended on consistently positive diversity effects on the periodic annual increment of the basal area. (Supplementary Tables 2 and 4, Fig. 1c and Supplementary Fig. 5). The absence of context dependency in forests could not be explained by overall differences in soil characteristics between the forest and grassland studies, which were located along similar soil gradients (Supplementary Figs. 6 and 7) that exhibited moderate differences in soil cation-exchange capacities ($P = 0.06$) and pH ($P = 0.02$; Supplementary Fig. 8).

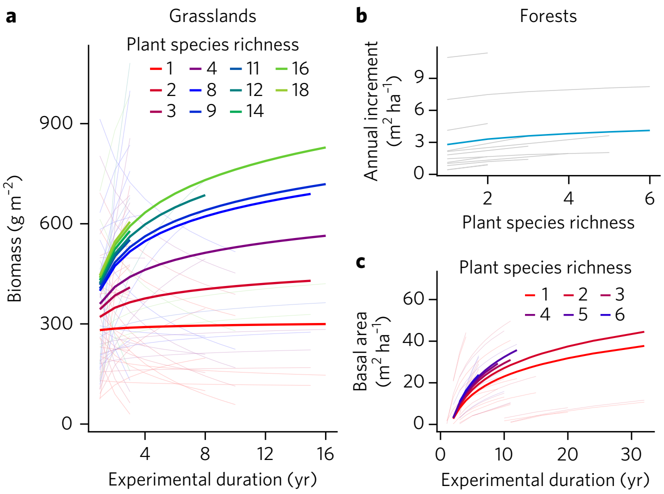

Fig. 1 | Ecosystem functioning in grassland and forest experimental ecosystems. a, In grasslands, trajectories of above-ground biomass (g m^{-2}) among plant species richness levels diverged over time. **b**, In forests, significant plant species richness effects on the periodic annual increment of the basal area (m^2 ha^{-1}) were consistent over time. **c**, The consistent positive effect of high-diversity communities on the periodic annual increment of the basal area may explain the temporal divergence in the total basal area among plant species richness levels. **a**,**c**, Lines are mixed-effects model fits for each plant species richness level within each study (thin lines) or across all studies (thick lines). **b**, Lines are mixed-effects model fits for each study (grey lines) or across studies (blue line). For grasslands, the above-ground biomass was significantly affected by species richness ($F_{1,5754.7} = 14.21$, $P < 0.001$) and the species richness × time interaction ($F_{1,5754.7} = 8.53$, $P < 0.01$). For forests, the periodic annual increment of the basal area was significantly affected by species richness ($F_{1,1433.1} = 10.07$, $P < 0.01$) and the total basal area was significantly affected by time ($F_{1,291.9} = 24.32$, $P < 0.001$) and the species richness × time interaction ($F_{1,291.9} = 18.39$, $P < 0.001$). See Supplementary Tables 2 and 4 for more information. Data from 14 grassland (1,045 plots, $n = 7{,}886$ measurements (plot by age combination)) and 12 forest experimental ecosystems (370 plots, $n = 1{,}887$ measurements (plot by age combination)) were entered in the analyses.

Our results show that positive tree diversity effects started early and accumulated through time. Thus, mechanisms associated with positive biodiversity effects on ecosystem functioning, such as complementarity, may play a key role even during the early stages of community assembly[25]. Decreases in ecosystem functioning in forests; for example, due to tree mortality[26], appear to be offset by higher growth of surviving trees. This differs from grasslands, in which community-level biomass is highly dependent on plant density[24]. Temporal divergence may continue to increase not only due to cumulative processes (as detected in our study), but also due to strengthening of competitive interactions[27]. The importance of

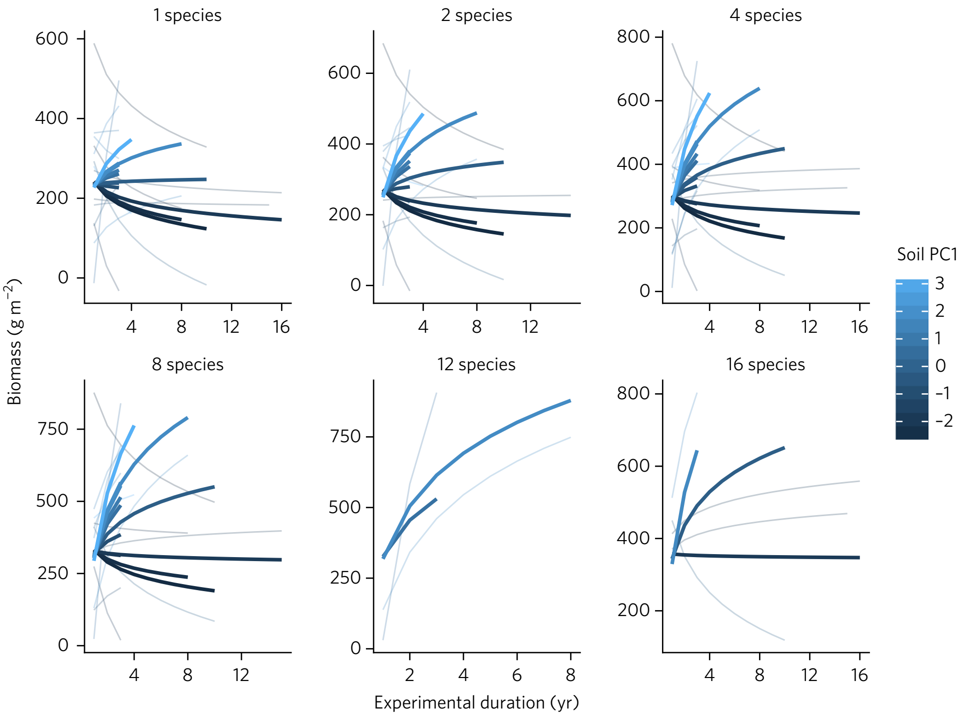

Fig. 2 | Influence of soil characteristics on temporal divergence in grasslands. The lines are mixed-effects model fits for each plant species richness level and soil characteristics within each study (thin lines) or across all studies (thick lines). The plots only show the temporal trajectories of plant species richness levels present in at least two experimental grasslands. The soil characteristics are based on a principal component analysis; the first principal axis (soil PC1) explained 48% of the variation when positive values were associated with higher cation-exchange capacity, soil organic carbon content and volumetric water content at the wilting point, and lower soil bulk density. For more information, see Supplementary Table 3 and Supplementary Fig. 2.

niche partitioning over time also may increase on smaller spatial scales[28] and thus may require longer to be detected at the plot level. Data availability from long-term studies and more diverse forest systems remains one of the main challenges for understanding temporal dynamics in forest experimental ecosystems. For example, the longest-running forest biodiversity experiments in this study usually had communities with only one or two species. Moreover, longer and multi-generation forest experiments may provide a better understanding of the effects that pathogen and herbivore attacks and the accumulation of soil pathogens may have on biodiversity effects through time. It is possible that temporal dynamics of biodiversity effects in forest ecosystems become increasingly similar to those of grasslands when compared at similar stages in terms of generations of the study organisms or under different soil characteristics; for example, sites with lower cation-exchange capacity and higher pH (Supplementary Fig. 8).

In conclusion, our results show a consistent temporal divergence of ecosystem functioning across plant diversity levels in both grassland and forest experimental ecosystems. In grasslands, temporal divergence was the result of a variety of patterns, all of which ultimately caused an increase in biodiversity effects over time. In contrast, temporal divergence in forests was not detected when ecosystem functioning was measured as a rate (the periodic annual increment of the basal area), but rather as an amount (the total basal area). Therefore, the increasing strength of the biodiversity–ecosystem functioning relationship in forests was related to an increase in function of high-diversity communities driven by a consistent positive effect of high-diversity communities on the periodic annual increment of the basal area. The temporal divergence in ecosystem functioning observed in our analysis may have multiple implications for the provisioning of vital ecosystem services in managed ecosystems. For instance, we need to determine other potential biotic and abiotic factors that drive either an increase in ecosystem function in high-diversity communities or a decrease in low-diversity communities over time. Such mechanistic understanding is fundamental as low-diversity plant communities are widely used in productive landscapes[18,19]. Overall, our results support the importance of management practices that reinforce the functional and structural complexity of ecosystems on different spatial and temporal scales[18] and, crucially, either attenuate decreases in function in grasslands or increase function in grassland and forest ecosystems.

Methods

Data acquisition and description. Long-term experiments that had manipulated plant species richness in grasslands and forests were identified using published meta-analyses, review papers on related topics and experimental platforms for biodiversity research (Supplementary Methods). Experiments were included if: (1) plant species richness was directly manipulated through sowing or planting and included monocultures of all species present in the mixtures, (2) raw data at least at the plot level were available, (3) above-ground plant biomass (in grassland) or basal area (in forest) data from at least three points in time from different years were available and (4) the experiment was conducted for at least three years in grasslands and five years in forests. For forests, the required experimental duration was longer than for grasslands because the establishment of tree-dominated experimental studies and the biodiversity effects on ecosystem functions were expected to take longer.

Data from 26 long-term biodiversity experiments met these criteria (Supplementary Table 1), including 12 forest experiments (370 plots, $n = 1{,}887$ measurements (plot by age combination) across experiments) and 14 grassland experiments (1,045 plots, $n = 7{,}886$ measurements (plot by age combination) across experiments). The annual peak above-ground biomass (g m^2) and basal area (m^2 ha^{-1}) were used in grassland and forests, respectively. In forests, we included two types of ecosystem function: the periodic annual increment of the basal area and the total basal area. The periodic annual increment of the basal area is a rate and is therefore more comparable to annual peak above-ground biomass in grasslands (see Supplementary Methods). The total basal area is an amount that captures cumulative tree growth. Both measures were used to quantify ecosystem functioning following the definition in Hooper et al.[3] (that is, ecosystem functioning includes ecosystem properties, such as process rates and the size of the compartments).

Temporal divergence. We used linear mixed-effects models to assess the temporal dynamics of ecosystem function among plant species richness levels using either plant above-ground biomass in the grassland experiments or the basal area in the forest experiments. We fitted a separate model for the grassland experiments using the annual peak above-ground biomass and two separate models for forest experiments—one using the total basal area and the other using the periodic annual increment of the basal area. The initial model included plant species richness, time and the interaction between richness and time as fixed effects in both the grassland and forest experiments. We then simplified the models by excluding non-significant fixed effects and interactions ($P > 0.1$). Plant richness was the sown or planted richness (natural logarithm) and time was the experimental age in years (natural logarithm). The natural logarithm transformation was used based on the expectation of fast, initial increases in ecosystem function, followed by constant growth in the later years of the experiment. Using a random slope and intercept structure, random effects included study, study × richness, study × time, study × richness × time and a term for plot within study for grasslands and for the total basal area in forests. The random structure for the periodic annual increment of the basal area included study, study × richness and a term for plot within study. We accounted for repeated measurements within plots by using a first-order autoregressive covariance structure, which fitted the data better than a compound symmetry covariance structure based on the Akaike information criterion. The best covariance structure was first-order autoregressive. The models were fitted with the asreml function in the asreml package in R and the results were extracted using the test.asreml function in the pascal package in R. Analyses were run in R version 3.2.4 (ref. [29]).

Effects of soil characteristics on temporal divergence. To explore the variation in temporal trends among the grassland studies, an additional model was tested that included species richness, time, soil characteristics and their interactions (Supplementary Methods). As a consistent set of soil variables was not available across the studies, we used data from SoilGrids250 (ref. [30]) to provide a general and consistent description of the study area. However, these data are proxies for site-specific quantitative information and need to be interpreted with caution. The soil characteristics were used to perform a principal component analysis, in which the first and second axes explained 48 and 40% of the variation across the grassland experiments, respectively (Supplementary Fig. 2). We did not analyse the effects of soil characteristics in the forest experiments because we did not find evidence of multiple trends underlying the temporal divergence (Supplementary Table 2 and Fig. 1b). To compare the potential differences in the range of soil characteristics between experimental ecosystems, we performed an additional principal component analysis including both forest and grassland studies (Supplementary Methods and Supplementary Figs. 6–8).

Code availability. R code of the linear mixed-effects models is provided in the Supplementary Methods.

Data availability. The data that support the findings of this study are available from the authors upon request.

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Author contributions

N.E. conceived the idea. N.E. and N.R.G.-R. developed the idea. A.H., B.W., C.Palmborg, C.Potvin, C.R., D.I.F., D.P., D.T., F.M., H.A., H.E.E., J.J.E., J.J., J.K., J.A.P., J.v.R. and P.B.R. contributed experimental data. N.R.G.-R. assembled the data. N.R.G.-R. and D.C. analysed the data with input from F.I., J.K. and A.H. N.R.G.-R. wrote the paper with substantial input from all authors.

Competing interests

The authors declare no competing financial interests.

Additional information

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